

A bug's tale: revealing the history, biogeography and ecological patterns of 500 years of insect invasions

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Abstract

The arrival of Europeans to the Americas triggered a massive exchange of organisms on a continental scale. This exchange was accelerated by the rapid increase in the movement of people and goods during the 20th century. In Chile, scientific and technical literature contains hundreds of records of non-native insect species established in different parts of the territory, from the hyperarid Atacama Desert to the Magallanes Region. Here, we analyse temporal trends, taxonomic diversity, biogeographic origin and main impacts of these species on different sectors in Chile from the European arrival to the present. Our task includes a review of old records in museum catalogues, libraries, collections, expedition records and catalogues. Almost 600 species of non-native insects have been reported to be established in Chile. Introductions started with the very arrival of Europeans to the central valley of Chile and underwent a huge acceleration in the second half of the 20th century. The order Hemiptera was the most prevalent amongst non-native insects. Most species are linked to agriculture and forestry. Species are of Palearctic origin in more than 50% of the records. In terms of temporal trends, the rate of established non-native species shows an abrupt increase at the beginning of the 1950s. This change may be associated with the strong development in agriculture and forestry in Chile after World War II and the increase in intercontinental air traffic. We believe that the understanding of past patterns of introductions is an important component in the design of current policies to minimise the impact of invasive insects.

Keywords

biological invasions, Chilean fauna, insect pests, invasive species, non-native insects

Introduction

The advance of civilisations, human migration and the proliferation of trade between different regions have led to a strong increase in species movement (Buckland 1981). This exchange was accelerated by the rapid increase in the movement of people and goods during the 20th century (Seebens et al. 2017). Indeed, the exchange of different species of insects has intensified in the last 200 years, together with the great trans-continental movements of people, goods and services (Mack et al. 2000; Chapman et al. 2017; Liebhold et al. 2017). Today, all countries have hundreds or thousands of non-native species established in their ecosystems (Mack 2003; Langor and Sweeney 2009; Seebens et al. 2017); however, in many cases, it is difficult to determine the origin, pathway and date of the introduction. Furthermore, recent estimates indicate that observational bias means that many non-native pest species still go unreported (Bebber et al. 2019).

Social and economic factors are key components in the increase in propagule pressure or species introductions (Santini et al. 2013; Bacon et al. 2014), whereas ecological and biogeographical factors are the main determinants of establishment (Santini et al. 2013; Schulz et al. 2019). In the first case, accelerated economic growth, the agricultural or ornamental use of non-native plants, connectivity (e.g. the number and availability of ports) emerge intuitively as important variables to explain the rate of insect species arriving in a new country (Dehnen-Schmutz et al. 2007; Hulme 2009; Banks et al. 2015; Chapman et al. 2017; Seebens et al. 2018; Bebbber et al. 2019). On the other hand, biogeographic similarity (including climatic similarity), host availability and community invasibility have been described as the most important factors to explain the establishment of new insect species (Shea and Chesson 2002; Bacon et al. 2014; Burns 2015; Schulz et al. 2019). Thus, it is the particular combination of these factors that will define the composition of the non-native fauna in a region. For example, the pool of non-native insects in a country could be dominated by species whose origins are in biogeographic regions with environmental conditions that match those of the new habitats. An alternative scenario is a pool of non-native insects that arrived using pathways mainly associated with the main economic activities of the country, regardless of their biogeographic origin.

In a similar vein, it is not only the species' identities that can reflect different processes structuring the non-native assemblages. Diversity of orders or families may or may not respond to ecological factors. Non-native insect assemblages can be a reflection of the global richness of these groups, with the representation of orders or families being proportional to their world richness or the non-native richness may be biased towards a group associated with some particular pathway, socioeconomic or ecological variables (Sailer 1978, 1983; Yamanaka et al. 2015; Liebhold et al. 2016; Bebbber et al. 2019).

In the Americas, the arrival of Europeans triggered a massive exchange of organisms on a continental scale. Accidental and intentional introductions of plants and animals promoted the establishment of new insect species, especially those associated

with crops of foreign origin (Prado 1991). In continental Chile (excluding oceanic islands), new food and crops were introduced in the 16th century (Prado 1991); however, few non-native insects were reportedly established in the country until the 19th century (Prado 1991; Artigas 1995; González 2012). Other pathways of introduction of insects were the establishment of ornamental plants, forestry, livestock and accidental transport in human baggage (see results). An important intentional pathway for insect introductions to Chile, especially during the 20th century, was the implementation of biological control programmes (González and Rojas 1966; Zúñiga 1985; Rojas 2005). The introduction of these beneficial insects was a response to the increasing impact that non-native pests had on food production.

In Chile, the scientific and technical literature contains hundreds of records of non-native insect species in different parts of the territory, from the hyperarid Atacama Desert to the Magallanes Region. Using this information, here we analyse the biological patterns of establishment of non-native insects to Chile from the first European arrival to the present. In particular, we analyse temporal trends, taxonomic diversity, biogeographic origin and main sectors impacted by each species. Through the description of these patterns, we can obtain a better understanding of the process involved in biological invasions over a timescale of centuries.

Materials and methods

Database

We collected records of non-native insects established in continental Chile from scientific articles, museums, libraries, collections, Chilean governmental reports, expedition records and catalogues. A primary online search using the words “exotic insect”, “invasive insect”, “insect pests” and “Chile” and their equivalents in Spanish was performed in Google Scholar. However, this search provided few results. For example, the Alien Species First Records Database 1.2 (Seebens et al. 2017) contains only 18 records of insects for Chile. We reviewed complete journal series and specialised sites (*Revista Chilena de Entomología*, *Acta Entomológica Chilena*, *Revista Chilena de Historia Natural*, *Anales de Zoología Aplicada*, *Boletín del Museo de Historia Natural*, *Gayana*, *Anales del Museo de Historia Natural de Valparaíso*, *Publicaciones Ocasionales del MNHN*, *Agricultural Técnica*, *Anales de la Universidad de Chile*, *ISC*, *EPPO Bulletin*, *EPPO Reporting Service*, *CABI*, *SAG Reports*, amongst others), specialised books (Prado 1991; Artigas 1995; CONAMA 2008, amongst others), museum and private collection catalogues and reports from expeditions (for a complete list, see the Supplementary files). We consulted specialist entomologists for some specific taxonomic groups. Most references were obtained (through loans or purchases) in a paper format outside Chile. When a mention of a non-native species was detected, we tracked back the literature for the original report. At least the page with the reference for each spe-

cies can be obtained in a digital format upon request from authors. First, we searched for explicit statements and dates of first records of non-native insects in the country. In some cases, we included the year of the first mention of the species in Chile when the authors explicitly recognised that the specific year of introduction or establishment is unknown. We selected the low limit when the publication indicates a range of years because reports usually are published several years after the real date of introduction/establishment of the species. We included species that were eradicated by governmental initiatives, but that were originally successfully established in the country. We collected species name, taxonomic position and year of first report. After we obtained our list, we completed our database by reviewing the literature to determine origin, type of impact and whether the species was used for biological control. For origin, we used the classification of biogeographic Realms from Olson et al. (2001). Given that a species can belong to more than one realm, we considered all realms including the native distribution ordered by area occupied in each one. For type of impact on human activities, we searched for publications where some type of direct and indirect impact was mentioned for the species. We included current and potential descriptions of impact in any country or region. In this sense, our classification was comprehensive and it does not mean that all these impacts have been reported in Chile, but the classes used are an approximated representation of the most critical areas/industries in the country. We used the following categories: agriculture, forestry, ornamental plants, environmental (impacts on biodiversity, endangered or endemic species or ecosystems), livestock, human health and infrastructure (damage to artificial structures, roads, ports, heritage buildings etc.). In some cases, when no description of impact was found in the scientific or technical literature, we recorded the impact as unknown (~ 5%).

Analysis

First, we estimated several descriptive statistics. We calculated the percentage of insects belonging to each order and family of non-native insects and also the distribution of orders as a function of the dominant realm of origin. We compared the frequency distribution of the number of species per order of non-native insects with the proportional number of insect orders in the world and Chile. For world data of insect richness, we used Stork (2018); for Chilean insect richness, we used CONAMA (2008). In addition, we compared the Palearctic component with the database of invasive insects of North America (Yamanaka et al. 2015). We only included in the analysis Palearctic species because Nearctic and Neotropical realms involve native species for each region and the other realms show too few species for a meaningful comparison. In the same vein, we estimated the frequency distribution of the number of species per type of impact.

We used the common species-time approach to examine temporal trends in insect dates of first report (e.g. Preston (1960); White (2004, 2007); White et al. (2006)). The accumulated number of species was calculated for the complete dataset, main orders (more than 40 species) and for those insects considered biological control species

(despite an intentional or accidental introduction). For the complete dataset and main orders, we evaluated three hypotheses of the temporal evolution in species accumulation (S). We compared linear, exponential and segmented trends. A linear accumulation suggests that the rate of accumulation is constant through time (t), independent of changes in population movement, economic growth and/or market changes (no acceleration). Exponential accumulation indicates that species accumulation shows a smooth acceleration ($S = a \cdot \exp(b \cdot t)$), where S is the number of species, t is time and a and b are parameters to be estimated. Finally, a segmented trend points to an abrupt change in the acceleration of species accumulation, which may be the result of abrupt changes in population movement, economic growth and/or market changes, amongst other factors. To avoid the noise due to few records in the first centuries, we started our analysis with the number of species accumulated to 1850. We tested these hypotheses by fitting each model to our dataset and selecting the best one using the Bayesian Information Criterion (BIC) in the R environment using function `lm` and `nls` (R Core Team 2022).

Results

Our review identified 591 non-native insect species established in Chile. Three of them were eradicated after establishment (see Suppl. material 1). From this total, we found the date of the first report for 572 species. The non-native insect fauna of Chile is dominated by the order Hemiptera, with almost 40% of the species (Fig. 1a). Coleoptera and Hymenoptera each represent approximately 20% of the total species (Fig. 1a). Amongst the families of Hemiptera, Aphididae (23% of all species) and Diaspididae (5%) were the most frequent. In Coleoptera, Curculionidae (7%) was the dominant family. The distribution of families in Hymenoptera was more homogeneous, with most species acting as a biological control agent of insect pests. The origin of the non-native species was strongly biased to Palearctic insects. Species from this realm represent more than 50% of the non-native insects. In a secondary position and well behind the Palearctic origin, Nearctic and Neotropical species made important contributions to the non-native insect fauna of Chile (Fig. 1b). For Palearctic, Australasian, Indomalayan and Nearctic species, the dominant order was Hemiptera (Fig. 1b, c). Only for Neotropical and Afrotropical species, Coleoptera was the dominant order (Fig. 1b, c). From the Palearctic component, 53% of the species already established in Chile are also established in North America.

When comparing the relative richness of the non-native insects established in Chile and world richness of species per Order, we observed a disproportionate representation of orders Hemiptera and Hymenoptera and a strong underrepresentation of the orders Coleoptera, Diptera and Lepidoptera (Fig. 2a). The same pattern was observed when comparing non-native established insects with Chilean native insect richness (Fig. 2b). Most non-native insects are described as having an impact on agriculture, forestry and

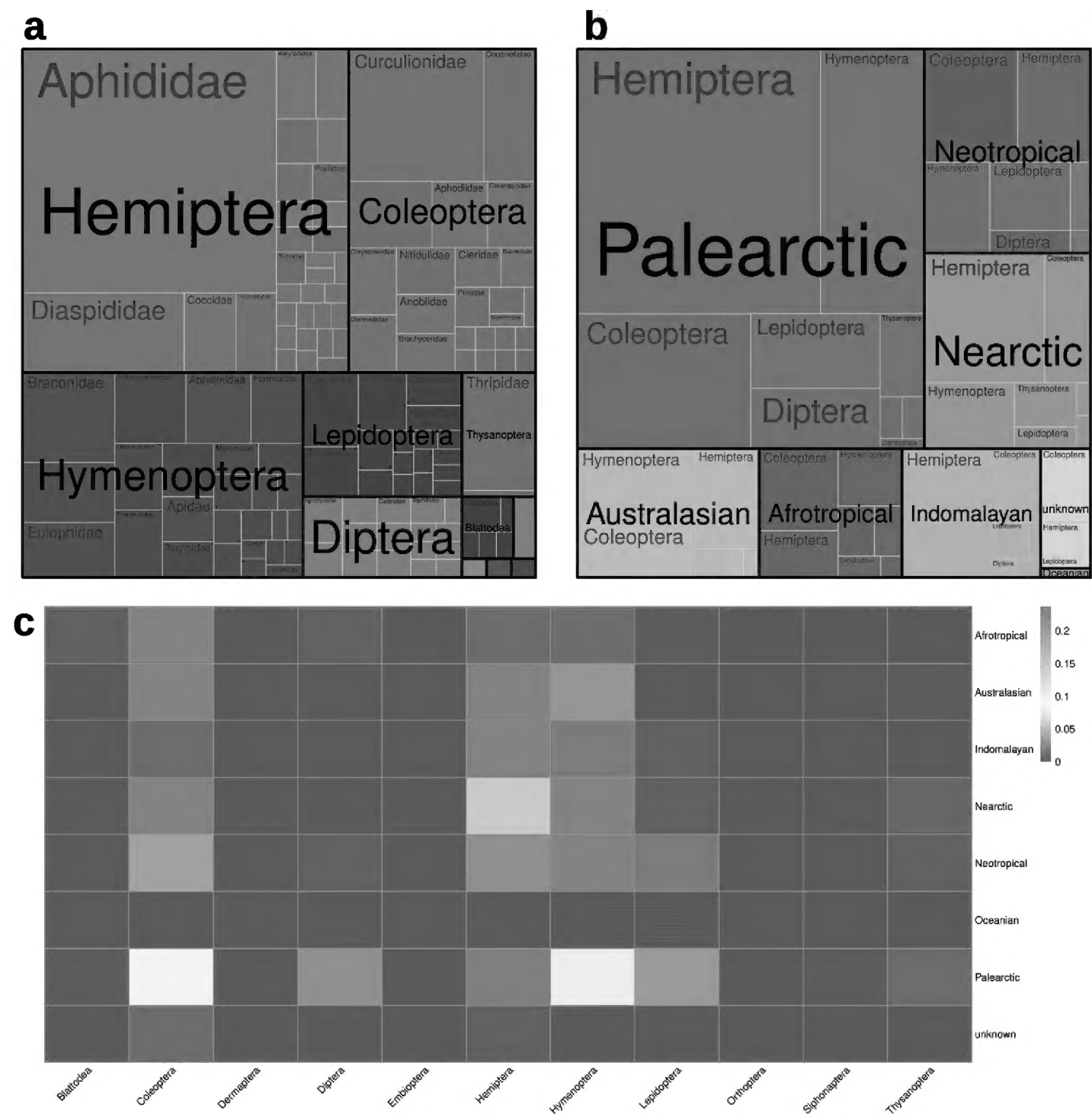


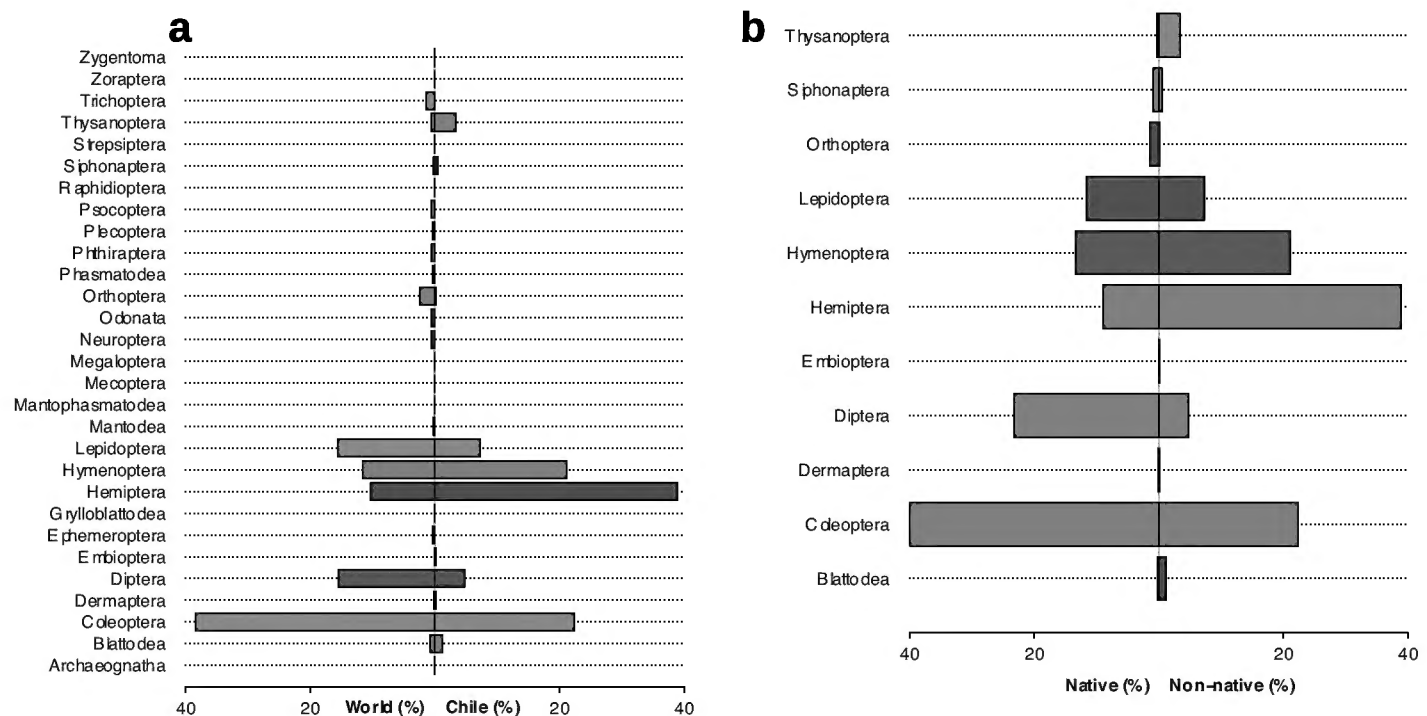
Figure 1. Taxonomic and biogeographic patterns of the non-native insect fauna of Chile **a** proportional representation of species belonging to each order and family **b** proportional representation of the biogeographic realms of origin of orders of the species **c** Heatmap showing the bivariate distribution (%) of orders and origins of the species.

ornamental activities (Fig. 3). The frequency of non-native species with an impact on other areas shows a minor representation. Biological control agents correspond to 17% of all species.

When we analysed temporal trends of the total accumulated number of non-native species, the best model was the segmented regression (Table 1). The best model showed an abrupt increase in the rate of non-native species recorded around 1949. Starting in that year, the species accumulation rate increased more than three times (Fig. 4a). When we look at the more abundant orders, we see that Coleoptera, Hymenoptera and Lepidoptera show the same pattern of increase (segmented model) (Table 1, Fig. 4b).

Table 1. Results for models fitted to the total number of accumulated non-native insects in Chile considering all species and the main orders separately.

All orders				
Model	Formula	Parameter	R ²	BIC
Linear	$S = a + b \cdot t$	$a = -6216; b = 3.310$	0.90	1472.7
Exponential	$S = a \cdot \exp(b \cdot t)$	$a \approx 0; b = 0.017$	0.99	1107.1
Segemented	$S_i = a_i + b_i \cdot t$, with $i = 1, 2$	$a_1 = -2797; b_1 = 1.512; a_2 = -11260; b_2 = 5.854$	0.99	1031.3
Coleoptera				
Linear	$S = a + b \cdot t$	$a = -1160; b = 0.624$	0.87	1136.0
Exponential	$S = a \cdot \exp(b \cdot t)$	$a \approx 0; b = 0.015$	0.99	837.0
Segemented	$S_i = a_i + b_i \cdot t$, with $i = 1, 2$	$A_1 = -399.7; b_1 = 0.221; a_2 = -2010; b_2 = 1.054$	0.99	746.0
Hemiptera				
Linear	$S = a + b \cdot t$	$a = -2104; b = 1.126$	0.82	1363.2
Exponential	$S = a \cdot \exp(b \cdot t)$	$a \approx 0; b = 0.019$	0.99	933.6
Segemented	$S_i = a_i + b_i \cdot t$, with $i = 1, 2$	$A_1 = -661.0; b_1 = 0.3611; a_2 = -4411; b_2 = 2.291$	0.99	1006.4
Hymenoptera				
Linear	$S = a + b \cdot t$	$a = -6216; b = 3.310$	0.71	1267.1
Exponential	$S = a \cdot \exp(b \cdot t)$	$a \approx 0; b = 0.017$	0.99	831.4
Segemented	$S_i = a_i + b_i \cdot t$, with $i = 1, 2$	$a_1 = -2797; b_1 = 1.512; a_2 = -11260; b_2 = 5.854$	0.99	788.2
Lepidoptera				
Linear	$S = a + b \cdot t$	$a = -6216; b = 3.310$	0.89	825.2
Exponential	$S = a \cdot \exp(b \cdot t)$	$a \approx 0; b = 0.017$	0.98	619.0
Segemented	$S_i = a_i + b_i \cdot t$, with $i = 1, 2$	$a_1 = -2797; b_1 = 1.512; a_2 = -11260; b_2 = 5.854$	0.98	557.9

**Figure 2.** Comparison of the frequency distribution of insect orders in the **a** World fauna and **b** Chilean fauna, with the pool of non-native insects established in Chile.

However, Hemiptera species accumulation shows an exponential increase (Table 1, Fig. 4b). The number of biological control agents shows an accelerated increase since the 1950s (Fig. 4c).

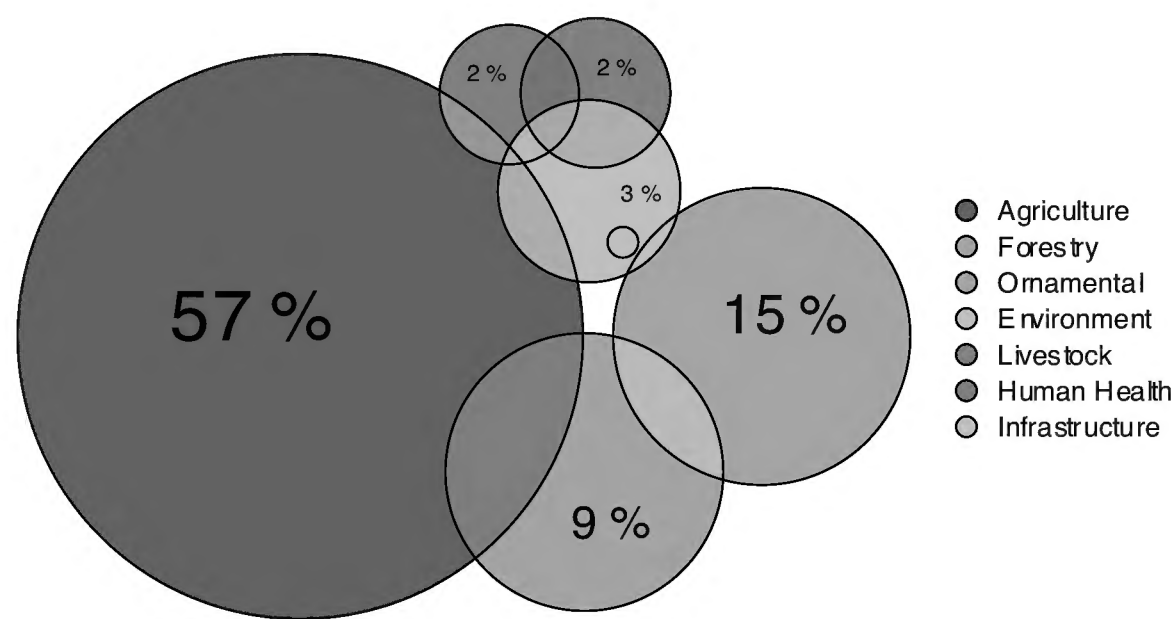


Figure 3. Percentage of non-native insect species established in Chile with the impact on each category of human activity, according to global literature. Unknown categories are not shown. Overlap areas correspond to the percentage of species with more than one category of impact (n = 565).

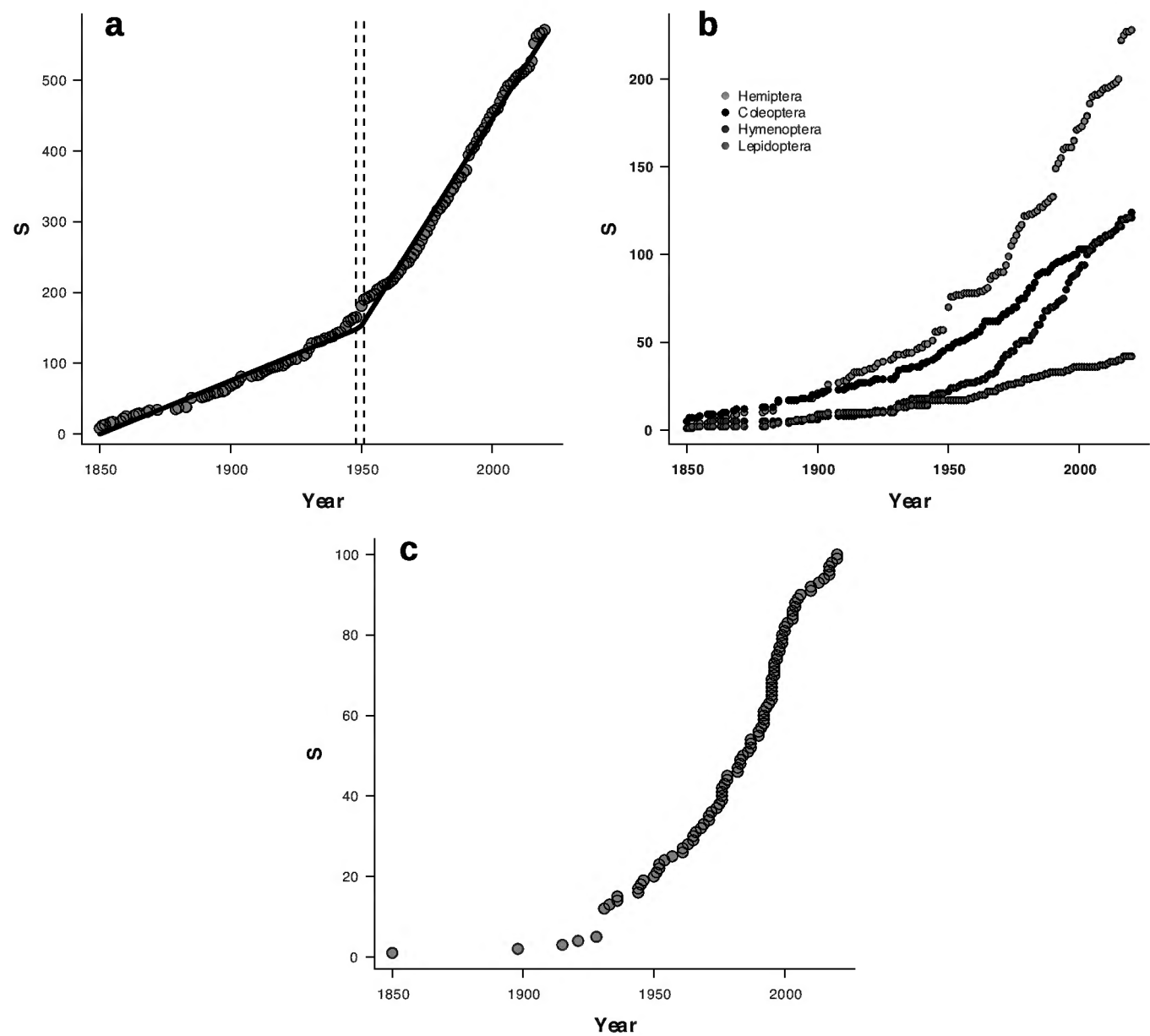


Figure 4. Temporal trend of the accumulated number of non-native species in Chile (S) **a** total number of species. Points correspond to observed data, the black line corresponds to the fit of the regression model and the dashed lines indicate the 95% confidence interval for the break-point in the segmented regression **b** number of species of the most abundant orders **c** number of species identified as biological control agents.

Discussion

The history of insect invasion in Chile follows the common trend observed all around the world (e.g. Sailer (1983); Yamanaka et al. (2015)). The arrival of Europeans to the country started major transitions in the insect fauna mainly due to the introduction of non-native plants. For example, the introduction of new crops, such as wheat, began as early as 1541. However, because most non-native plants were introduced as seeds, few insects were detected and very few became a phytosanitary issue before the 19th century (Prado 1991), a similar situation to the one described by Sailer (1983) for the USA. Fruit crops and vines were also introduced early on in colonial times (Lacoste 2004; Lacoste et al. 2011), but major pests of these crops also arrived in Chile during the 19th and 20th centuries (Artigas 1995; González 2012).

Our results show that the composition of non-native insect fauna in Chile is strongly biased to groups associated with agriculture and forestry. This is a common situation in other parts of the world (Bradshaw et al. 2016; Liebhold et al. 2016). For example, Sailer (1978, 1983) and Yamanaka et al. (2015) also showed that most non-native species in North America belong to the order Hemiptera. Waage et al. (2008) also found that Hemiptera (Homoptera in the original) is the order with the most species introduced in Europe and Africa. According to Stork (2018), Hemiptera globally is only the fifth order in terms of the number of species, but it is the most intercepted order in borders of several countries of the world because its association with crops, forestry and fruit or ornamental trees (Gippet et al. 2019; Turner et al. 2021).

In terms of the origin of the non-native insects, most of them show a Palearctic origin. Again, this situation has been observed in other parts of the world. Miller et al. (2005) described similar results when they analysed the richness of non-native scale insects in the USA, all of them associated with agriculture. Yamanaka et al. (2015) also found that, in North America and Japan, most of the non-native insects are of Palearctic origin. This result is not surprising given that more than 50% of the non-native plants in Chile are of European origin (Fuentes et al. 2014). Barriga et al. (1993) and Fuentes-Contreras et al. (1997), in their analyses of Coleoptera and Aphids, respectively, report that, with only two exceptions, non-native insects feed on non-native plants, which supports the hypothesis that the non-native-plant/non-native-insect association is the key promoter of the introduction of arthropods (Liebhold et al. 2018). This is reinforced by the fact that most non-native insects are associated with agricultural, forestry and ornamental plants. Moreover, most early alert systems in the world have been designed to detect non-native insects of economic importance (agriculture, forestry etc.).

We detected an abrupt increase in the rate of introductions recorded around 1950. Many studies have shown an exponential increase in the rate over years, especially in the last century (see examples in Seebens et al. (2017)) and even the timing of this acceleration has been observed in other taxa at global scale (Seebens et al. 2017). In our case, this abrupt change can have several explanations. First, the change in the rate can be a by-product of the increase in Hemiptera introductions in the same years following

the growth in agricultural production post-World War II during the “Green Revolution” (Díaz et al. 2016). Bonnamour et al. (2021) describe this moment as the second wave of globalisation, where international trade began to increase significantly. A second explanation comes from the major development of biological control programmes of plant pests in Chile in the second half of the 20th century, with particular relevance for the parasitoid Hymenoptera (Rojas 2005). Both explanations make reference to changes in agricultural production, but a third alternative is related to the strong increase in air transport (Díaz et al. 2016). The use of international air transport by Chileans showed a marked, strong growth at the beginning of the 1950s. Furthermore, international trade in Chile also increased in the last decades of the 20th century, along with globalisation. In particular, such a recent increase in trade with Asian countries could be incorporating new regions with new pools of potential invasive species (Seebens et al. 2018). Finally, observational bias in the report of new non-native species is probably present in our analyses (Bebber et al. 2019). For example, at the beginning of the 1950s and 1990s, three specific reports seem to add a significant number of records, creating jumps in the accumulated series (Essig 1953; Prado 1991; Starý et al. 1993). However, the segmented model detects changes in the intercept and slope of the two segments of the series. Reports of new non-native species of insects require trained entomologists and international collaboration with specialist taxonomists. For Chile in the 19th century, these human resources were a few foreign naturalists working in the country. The first applied entomologists appeared at the end of 19th and the first half of the 20th century. Finally, a more robust and permanent process of training and networking of applied entomologists and agriculturalist scientists was promoted only during the second half of the 20th century (Artigas 1995; del Pozo et al. 2021). All these variables might be associated with the increase in non-native species, but more detailed analyses are needed to evaluate their relative contribution.

Nowadays, climate change has acted as a promoter of the range expansion of many insect species. For non-native species, ongoing and future climate change could facilitate the short distance dispersal of non-native insects across national borders (Pearson 2006; Hulme 2017). However, for some authors, climate-tracking species should not be considered non-native or invasive (Urban 2020).

Conclusions

In this study, we reconstructed the main patterns of insect introductions to Chile. The order Hemiptera was the most prevalent amongst non-native insects, with species linked to agriculture and forestry industries. Species are of Palearctic origin in more than 50% of the records. Temporal trends show an abrupt increase at the beginning of the 1950s. This change may be associated with the strong development in agriculture and forestry in Chile after World War II and the increase in intercontinental air traffic. We believe that the understanding of past patterns of introductions is an important

component in the design of current policies to minimise the impact of invasive insects. This database is the first attempt to compile this information, but this is essentially a work in progress. It has to be updated and improved by governmental agencies, academics and specialists for a better understanding of it. We think that some of the results presented in this study may be representative of other countries in South America. Similarities with other regions suggest that the processes behind insect introductions are common around the world and their detailed description can be a fundamental tool for managing current introductions and preventing major economic, social or environmental damage.

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Supplementary material I

Database: exotic insects of Chile

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Data type: table (excel file)

Explanation note: Excel file containing records of exotic insects in Chile.

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